THE FITNESS CONCEPT IN EVOLUTIONARY BIOLOGY: PHILOSOPHICAL AND SCIENTIFIC ASPECTS

Programme of talks

Wednesday 27th March

Hanna Kokko (Zurich) 9.15-10:15

The stagnation paradox and the alignment (or not) of individual and population fitness

Depending on who you ask, adaptation is expected to improve population fitness or not, and this difference in expectations seems to correlate with how much a person spends time thinking about evolutionary conflicts and/or density dependent population regulation. I will elaborate on these themes with a look at some of my own past and present modelling work, including examples where adaptation to seasonal environments and climate change produces counterintuitive results.

Alan Grafen (Oxford) 10:15-11:15

The Crucial Role of the concept of Fitness in Biology

The many arguments about fitness suggest it plays a crucial role in biology. Here, I try to articulate what that role is, in terms of three significant subdisciplines. First, ideas of Darwinian imply an individual-level variable that we now call fitness, as the quantity that natural selection improves. Second, empirical work that employs design includes most behavioural ecology,

functional morphology and functional anatomy: sometimes biologists lack detail to know, for example, how to balance a reduction in fecundity against an increase in survival. Third, population genetic models nowadays may have "fitness components" as parameters, such as survivorships and fecundities. The challenge in my 'formal darwinism project' is to build as realistic a population genetic model as possible, with the goals of showing that (under reasonable assumptions) we can construct an individual-level variable called fitness, that natural selection does act to improve mean fitness, and of showing how tradeoffs can be evaluated.

Break

Samir Okasha (Bristol) and Bengt Autzen (Cork) 11:45-12:45

The Concept of Fitness: a philosophy-of-science perspective.

Fitness is one of the most fundamental concepts in evolutionary biology, as it is intimately connected with evolution by natural selection. Despite this, the fitness concept is somewhat elusive, as a number of authors have noted, seemingly lacking a fully general definition; and there is a sizeable literature devoted to fitness in both biology and philosophy of biology alike. In some ways this is rather odd, since natural selection is seemingly a simple and well-understood process. Here we try to make sense of this situation. We argue that fitness is a theoretical concept of modern biological science. Following a long tradition in philosophy of science, we argue that theoretical concepts are defined by their *theoretical role,* and we distinguish between a role and a *realizer* of that role. What then is the role of fitness in the theory of evolution? We argue that fitness in fact plays three (distinct but related) roles, two of which pertain to the *process* of natural selection and one of which pertains to its *product*. Moreover, under different model assumptions, the quantities (or theoretical magnitudes) that realize these roles may coincide, or they may not. We use this framework to shed light on a number of controversies surrounding fitness.

Lunch

Grant Ramsey (Leuven) 1:45 – 2:45

Fitness and Variance in Offspring Number

The philosophy of evolutionary biology has for more than three decades taken it for granted that variance in offspring number depresses fitness and is therefore selected against. The conclusions drawn from the idea that variance depresses fitness are many and profound. Some have suggested that because of this fitness requires a new mathematical foundation, whereas others draw the more extreme conclusion that fitness is therefore not a causal property. In this talk, I examine the source of the idea that variance affects fitness and show that it rests on conceptual and mathematical errors.

Ellen Clarke (Leeds) 2:45 – 3:45

The concept of the evolutionary individual as an idealised theoretical model

Recent work on scientific modelling has largely converged on the view that models gain at least part of the predictive and explanatory power by idealising their target system, rather than by trying to faithfully represent it. That is, aspects of the target will be ignored, exaggerated or distorted in ways that increase the modal power of the model. For example, evolutionary populations are modelled as being infinite in size, ideal gases as undergoing frictionless collisions. I argue that we can cast light on the role of natural kind concepts in science by understanding them as conceptual models. In particular, i'll detail some ways in which we idealise living organisms to generate a concept of an evolutionary individual which serves theoretical purposes in evolutionary biology via the theoretical property, fitness.

Break

Sean Rice (Texas) 4.00 – 5.00

The future is a random variable

The number of descendants that an individual will contribute to future populations, and the phenotypes of those descendants, cannot be known with certainty until after the fact. Both fitness and offspring phenotype should thus be treated as random variables -- having distributions of possible values. I will briefly discuss some mathematical tools that allow us to treat fitness as a random variable, and then highlight some evolutionary outcomes that arise only when we introduce stochasticity into our models of evolution

Thursday 28th March

Andy Gardner (St Andrews) 9.15 – 10.15

The rarer-sex effect

I will discuss the historical development of the theory of the “rarer-sex effect”—the basic Darwinian explanation for why, in many species, there are approximately equal numbers of males and females at birth—which has proceeded largely through refinement of conceptualisation of the fitness consequences of sex ratio.

John McNamara (Bristol) 10:15 – 11:15

Genes versus individuals

One might expect natural selection to lead to a population in which the resident genes are maximising their rate of spread within the environment they help create. But what does this say about the behaviour of the individuals that carry the genes? Usually, the characterisation is in terms of some form of individual maximisation. I highlight the relationship in various contexts. In doing so, I wish to question to what extent the individual optimisation perspective is both conceptually useful and of practical use as a modelling tool. In particular, I will present a model of the timing of germination of a seed in spring. This case raises some interesting conceptual issues, as well as highlighting the relationship between genes and the individual.

Break

Mauricio Suarez (Madrid) 11:45 – 12:45

The Complex Nexus of Fitness

Fitness is often understood to be a probabilistic disposition, or propensity. There are undoubtedly strong intuitions behind this understanding, which have to do with how fitnesses manifest themselves in ecological environments. It is moreover an understanding that preserves the concept's intended explanatory role. However, every attempt to fill in its details gives rise to manifold problems. Some of the problems are philosophical, and relate to the causalist-statisticalist dispute. Yet more pressing issues, however, relate to empirical findings regarding fitnesses across generations and the higher moments of the statistical distributions that putatively represent them. I suggest that a look at the philosophy of probability literature may help. The so-called propensity interpretation of probability championed by Popper has essentially long been abandoned - as has Popper's associated attempt to solve the paradoxes of quantum mechanics. Instead, I have suggested a complex nexus of chance account of both fitnesses and quantum properties. I review the central element of this acount, the tripartite conception of chance, and argue that it offers a response to some of the challenges.

Lunch

Hannah Rubin (Missouri) 1:45 – 2:45

Symmetries in Evolutionary Dynamics

Models of evolutionary change typically use some quantity called “fitness” which measures an organism’s reproductive success. But what exactly does it mean that fitness is such a measure? Exploring the significance of *symmetries*, features of a system that remain unchanged under some kind of transformation, illuminates some answers. I will discuss two projects on symmetries in evolutionary dynamics. First, I will discuss a project with Simon

Huttegger and Kevin Zollman which uses tools from measurement theory to show that whether certain statements about fitness are or are not meaningful (e.g., saying something is 'twice as fit') depends on the features of a model one thinks are important to preserve and the dynamical equations employed. Second, I will discuss a project that uses concepts from philosophy of physics to expound on the value of *reformulations,* fitness calculations that exploit symmetries in the system: they agree on what the world is like and give equivalent predictions of evolutionary change (e.g., inclusive and neighbor-modulated fitness). I will argue that there are epistemic gains from reformulation; that is, it gives us new knowledge of evolution.

Thomas Hansen (Oslo) 2:45 – 3:45

Fitness as a random variable

I will start from the premise that fitness needs to be understood in terms of its use in the mathematics of natural selection. Mathematically, selection can be described as a mapping from one set of items to another set of items. Items are grouped in types, and the fitness of a type is the amount (number of items) of the type after selection divided with the amount before selection. In finite populations this makes fitness a random variable with a type-specific distribution. I present this as a generalization of the propensity interpretation of fitness. On this basis I criticize some standard mathematical and philosophical descriptions of fitness in finite populations. Finally, I discuss the evolvability of fitness.

Break

Marshall Abrams (Birmingham, Alabama) 4.00 – 5.00

Long-term trait fitness and population-environment systems

Philosophers of biology have usually assumed that trait fitness is rooted in objective probabilities associated with actual, particular (token) organisms. In my book Evolution and the Machinery of Chance, I argued that this "propensity interpretation of fitness" (PIF) tradition conflicts with the way that empirical research in evolutionary biology works. The PIF tradition bases fitness on the idea that a token organism in its circumstances is a chance setup, a complex analogue of a dice tossing configuration. I argue that making sense of evolutionary biology requires treating a population in its environment—a "population-environment system"—as the chance setup relevant to evolution. By distinguishing between roles that fitness plays in empirical research, I argue that though some varieties of fitness are measured on particular individual (token) organisms, evolutionary biology has no significant role for the causal, probabilistic fitnesses attributed to token organisms in the PIF tradition. The kind of trait fitness that matters to evolution is realized by a population environment system as a whole. After reviewing some of my previous arguments, I give a new argument for the population-environment conception. Pence and Ramsey developed a concept of trait fitness that avoids many problems with earlier PIF-based fitness concepts. I argue that when we try to

apply this concept of trait fitness to a realistic range of evolutionary scenarios, it turns out that long-term trait fitness can't be defined in terms of token organisms' fitnesses, but is more readily understood as a property of a population-environment system. My argument for these points applies to other concepts of fitness designed to reflect longer-term changes, and suggests that some motivations for a more "organism-centered" biology can be used to support the population-environment conception—despite the origin of this conception in population-based modeling.